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THE EFFECT OF SCARIFICATION, LEACHING, LIGHT, STRATIFICATION, OXYGEN AND APPLIED HORMONES ON GERMINATION OF *PROTEA COMPACTA* R.BR. AND *LEUCADENDRON DAPHNOIDES* MEISN.

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Abstract

Both the seed coat and the embryo appear to contribute to the dormant condition in *P. compacta*. Germination can be improved to a greater or lesser extent by scarification, high oxygen tensions, stratification and applied hormones.

In *L. daphnoides* dormancy is mainly imposed by the seed coat which apparently acts as a barrier to oxygen diffusion to the embryo. A considerable increase in germination is brought about by scarification and high oxygen tensions applied to intact seeds. Stratification and applied hormones improve germination to a lesser extent.

Leaching and light treatments failed to improve germination in both species.

It is postulated that treatments promoting increased oxygen uptake enhance the metabolic activities of the embryos. These activities result in changes in the hormone levels in the embryo which promote radicle elongation in *P. compacta* and cotyledon expansion in *L. daphnoides*.

Uittreksel

DIE EFFEK VAN SAADBESKADIGING, UITLOGING, LIG, STRATIFIKASIE, SUURSTOF EN TOEGEDIENDE HORMONE OP DIE ONTKIEMING VAN *PROTEA COMPACTA* R.BR. EN *LEUCADENDRON DAPHNOIDES* MEISN. Dit wil voorkom asof beide die saadhuid en die embrio van *P. compacta* bydra tot die russtand van die saad. Ontkieming word tot 'n mindere of meerdere mate bevorder deur saadhuid beskadiging, hoë suurstof konsentrasies, stratifikasie en toegediende hormone.

In die geval van *L. daphnoides* is die russtand waarskynlik geheel en al toe te skryf aan die feit dat die saadhuid die diffusie van suurstof na die embrio belemmer. Wanneer die saadhuide beskadig word of die intakte saad aan hoë suurstof konsentrasies onderwerp word, word 'n groot toename in ontkieming te weeg gebring. Stratifikasie en toegediende hormone beïnvloed ontkieming tot 'n mindere mate.

Uitlogings-en lig behandelings het nie die ontkieming van die twee spesies bevorder nie.

Daar word voorgestel dat behandelings wat suurstof opname versnel, die metaboliese aktiwiteit van die embrios verhoog. As gevolg hiervan verander die hormoon konsentrasies in die embrios, en dit lei tot die verlenging van die kiemwortel van *P. compacta* en die vergroting van die saadlobbe van *L. daphnoides*.

Introduction

Poor germination is common within the South African Proteaceae (Vogts, 1960; Horn, 1962; Van Staden, 1966; Brown and Van Staden, 1971). This has been attributed to the presence of endogenous inhibitors (Vogts, 1960), and ineffective seed screening methods (Horn, 1962). However, germination is poor

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even with improved sorting (Van Staden, 1966; Brown and Van Staden, 1971). Although Horn (1962) did not regard inhibitors as being of importance in preventing germination, recent reports (Brown and Van Staden, 1971; Van Staden and Brown, 1972) showed that aqueous extracts of proteaceous seed contained substances that could inhibit the germination of both lettuce and water cress. Whether these inhibitors are involved in the regulation of germination, and are leached as postulated by Vogts (1960), is not known. Other than a report that light and low temperature do not increase germination (Horn, 1962), no attempt has been made to investigate the effect of any of the treatments commonly applied to overcome dormancy. The present work describes the effect of scarification, leaching, light, stratification, oxygen and applied hormones on the germination of seed of two species.

MATERIALS AND METHODS

Seed of *Protea compacta* R.Br. and *Leucadendron daphnoides* Meisn. was obtained from the South African Department of Forestry. This was hand sorted and only plump, undamaged seed used. These were germinated in petri dishes on acid washed sand (40—100 mesh) which was kept just moist with distilled water. Because temperatures above 20°C have a detrimental effect on germination (Brown and Van Staden, 1971), seed was germinated at alternating temperatures of 10°C for 16 hours followed by 20°C for 8 hours. Light (ca. 1 $\mathrm{lm/m^2}$) was supplied by cool white fluorescent tubes to coincide with the higher temperature period.

The protrusion of the radicle through the covering structures was used as the criterion for germination. The effect of ineffective seed sorting was further eliminated by dissecting all ungerminated seed at the end of the experimental period, and expressing the germination results as a percentage of seed that contained fully developed embryos.

RESULTS AND DISCUSSION

Mode of germination

The fruit (hereafter referred to as the "seed") in *Protea* and *Leucadendron* is an achene. The embryo is surrounded by an inner membranous testa and an outer woody pericarp of varying thickness; being thinner at the radicle end than elsewhere. In *P. compacta* the seed is elongated (ca. 15 mm long and 7 mm wide) and covered with a dense layer of fine hairs. In contrast that of *L. daphnoides* is flattened with smooth sides (ca. 9 mm long and 10 mm wide). From the side it appears to be almost circular in outline.

The mode of germination of the two species differs. In *P. compacta* the first visible sign of germination is the protrusion of the radicle through the pericarp (hereafter referred to as the "seed coat"), while in *L. daphnoides* this only occurs after the seed coat has split. This splitting of the coat is very characteristic and always starts at the "radicle end" and extends along the edge of the flattened sides of the seed. This suggests that radicle elongation is preceded by cotyledon expansion and that without this, the radicle would not be able to emerge from within the seed coat.

Scarification treatments

When dormancy is imposed by the covering structures of the seed their complete or partial removal often results in increased germination (Barton, 1965). The coat may offer a mechanical restriction to radicle elongation or embryo enlargement (Barton, 1965; Esashi and Leopold, 1968) or alternatively it can exert its influence by acting as a barrier to the diffusion of oxygen and/or water (Barton, 1965; Edwards, 1968). The presence of hard woody coats in the species under investigation suggested that dormancy could be coat imposed.

Seed was mechanically scarified by filing away small portions of the coat. The treatments were as follows: (i) coat scarified at the "radicle end"; (ii) coat scarified at the "style end"; (iii) coat scarified midway on the side of the seed, and germinated with the scarified surface facing upwards; and (iv) the seed coat completely removed.

TABLE 1

THE EFFECT OF SCARIFICATION OF THE SEED COAT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES*

Figures are mean percentages of 8 replications of 10 seeds over 40 days.

SCARIFICATION TREATMENTS	*PROTEA COMPACTA*	*LEUCADENDRON DAPHNOIDES*
Intact seed	50 ± 5	30 ± 5
Scarified at "style end"	78 ± 5	90 ± 5
Scarified at "radicle end"	80 ± 3	75 ± 6
Scarified on side between "style" and "radicle ends"	45 ± 3	88 ± 2
Excised embryos	30 ± 8	30 ± 0

The results in Table 1 show that while scarification on the side of the seed had no effect on the germination of *P. compacta*, germination was significantly increased when portions of the coat at either end of the seed were removed. Such treatment could either weaken or remove the mechanical effect of the seed coat. When the coat was weakened by scarifying at the style end, "abnormal" germination, where the extending radicle pushed the cotyledons out of the covering structures, frequently occurred. Scarification on the side did not improve germination, possibly because the mechanical forces exerted by the coat were not altered sufficiently to allow the embryo to develop. These results suggest that the dormant condition of *P. compacta* is, at least in part, brought about by the mechanical restriction of the embryo by the seed coat. Where germination does not occur, the radicle is probably unable to develop sufficiently to rupture the coat. If this were the case it might be expected that complete removal of the seed coat would result in maximal germination. However, few excised embryos germinated, as exposure to the atmosphere made them particularly subject to microbial attack. The finding that few excised embryos of *P. compacta* germinate under sterile conditions *in vitro* suggests that embryo dormancy also contributes to the dormant condition (Van Staden, Brown and Button, 1972).

In contrast with *P. compacta*, all scarification treatments resulted in significant increases in the germination of *L. daphnoides* (Table 1). In the latter species the mode of germination did not deviate from that characteristic for intact seed, irrespective of the site of scarification. Furthermore scarification in the radicle region of the seed did not enhance radicle emergence from within the coat. This indicates that the events leading to germination follow a set pattern. The first visible sign of germination being the splitting of the seed coat, apparently as a result of cotyledon expansion, followed by radicle elongation.

To obtain information about the mechanism by which the seed coat imposes dormancy on seeds of *L. daphnoides*, scarified seed was germinated in two positions. When the scarified surface was placed on the sand, only 30% germination was recorded. However, 80% germination was obtained with the scarified surface uppermost. These results suggest that exposure to the atmosphere is beneficial in increasing germination. This was tested by covering the exposed surface with lanolin, a procedure which resulted in a reduction of germination to 50%. These results suggest that the seed coat of *L. daphnoides* acts as a barrier to oxygen uptake. In addition it is significant that when the scarified surface was placed downwards on the sand, a treatment that would favour leaching of compounds from the embryo, germination was reduced to a level equal to that of the controls.

Microbial attack is probably responsible for the low levels of germination observed in excised embryos. This is suggested by the fact that embryos that germinated did so within the first twelve days of the experiment, during which time microbial activity was not very marked.

The results lead to the conclusion that dormancy of *P. compacta* is partly a result of the mechanical restriction of the coat to radicle extension and partly due to embryo dormancy. In *L. daphnoides* however, dormancy appears to be mainly coat imposed. The coat apparently exerts its influence by restricting oxygen diffusion to the embryo. Further experiments were carried out to verify these findings.

Leaching treatments

Coat imposed dormancy may be due to the presence of inhibitors in the coat (Bradbeer, 1968; Irving, 1968) or alternatively their outward diffusion from the embryo may be impeded (Webb and Wareing, 1972). Although Vogts (1960) has postulated that inhibitors are involved in the regulation of germination of proteaceous seed, and such compounds have been extracted from the seed (Van Staden and Brown, 1972), their actual involvement in imposing dormancy has not been shown.

The effect of leaching on germination was investigated by the following procedures: Seed was shaken in 100 ml distilled water for 4, 8 and 12 days respectively. During this time the water was renewed every 2 days. The bulked leachates were concentrated to 100 ml, their pH adjusted to 2,0 upon which they were extracted and assayed for inhibitors as previously described (Van Staden

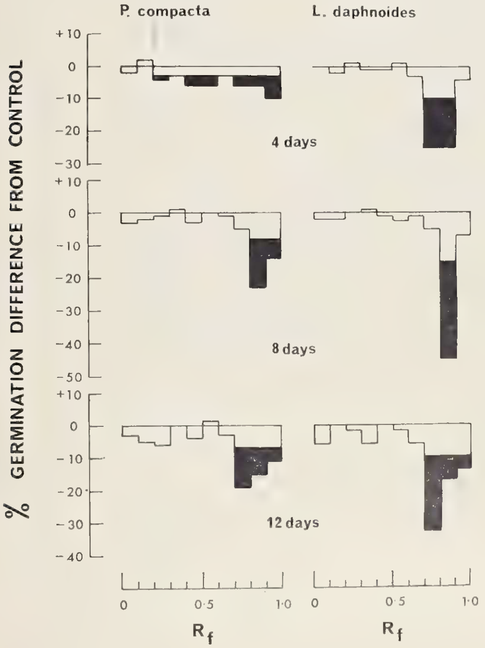

FIG. 1.

THE EFFECT OF SEED LEACHATES OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* ON GERMINATION OF GRAND RAPIDS LETTUCE SEED IN LIGHT.
Fifteen grams seed leached. Shaded areas represent differences significant at the 1% level.

and Brown, 1972). In Figure 1 it can be seen that inhibiting substances were removed from the intact seed by leaching. The inhibition produced by leachates increased up to 8 days, whereafter it remained more or less constant. Most of the inhibiting activity was found between R_f0,8 and 1,0, which corresponded with that previously reported for embryos and seed coats (Van Staden and Brown, 1972). In spite of the evidence indicating removal of inhibitors by leaching, the treatment did not increase germination (Table 2). Although this suggests that the inhibitors may not be active in regulating germination the low germinability may be the result of other factors related to the treatment, such as oxygen stress.

Table 2

THE EFFECT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* OF LEACHING SEEDS BY SOAKING IN DISTILLED WATER. Figures are mean percentages of 8 replications of 25 seeds over 63 days.

TIME (DAYS)	*PROTEA COMPACTA*	*LEUCADENDRON DAPHNOIDES*
0	49 ± 11	27 ± 1
4	6 ± 1	11 ± 1
8	2 ± 1	4 ± 1
12	0	7 ± 1

To eliminate inadequate aeration seed was leached intermittently (12 hours each day) in running water for 4, 8 and 12 days respectively. Care was taken that they never dried out. Under these conditions it was considered that seeds would receive sufficient aeration for germination. However, subsequent germination showed the same pattern as seed that was submerged in water (Table 3).

Table 3

THE EFFECT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* OF INTERMITTENT LEACHING OF SEED IN RUNNING WATER. Figures are mean percentages of 8 replications of 25 seeds over 63 days.

TIME (DAYS)	*PROTEA COMPACTA*	*LEUCADENDRON DAPHNOIDES*
0	45 ± 8	26 ± 4
4	20 ± 4	9 ± 2
8	17 ± 4	6 ± 1
12	9 ± 2	9 ± 2

If the dormant state of the seed is the result of high inhibitor concentrations in the embryos that cannot be leached through the seed coat, then scarification and placement of the seed in a position to favour leaching would be expected to increase germination. Such a treatment applied to *L. daphnoides* gave germination no different to intact controls. According to the evidence obtained it would appear as if the seed coats do not exert an influence on germination by impeding the leaching of inhibitors. If inhibitors play a rôle in the control of germination it is apparently not an over-riding effect.

The fact that the germination of both species is progressively inhibited with increasingly high levels of hydration (Tables 2 and 3) is probably due to the phenomenon of "water-sensitivity". Here a state of dormancy in induced by an over-abundant supply of moisture (Hay, 1962). According to Hay (1962) and Negbi, Rushkin and Koller (1966) this inhibition of germination is due to the resistance of the water layers to diffusion of oxygen into the embryo.

Stratification treatments

Van Staden *et al.* (1972) have shown that in *P. compacta* germination is only partly regulated by the seed coat because a large proportion of excised embryos do not germinate when placed under favourable conditions for germination. In *L. daphnoides* dormancy appears to be wholly coat imposed. It is well known that embryo and coat imposed dormancy may be overcome by a period of storage under moist conditions at low temperature (Wareing and Saunders, 1971).

TABLE 4

THE EFFECT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* OF INCUBATION OF SEED UNDER MOIST CONDITIONS AT 5°C AND 25°C

Figures are percentages of 250 seeds.

TEMPERATURE	TIME (DAYS)	*PROTEA COMPACTA*	*LEUCADENDRON DAPHNOIDES*
	0	46	20
5°C	30	59	30
	60	59	23
	90	65	18
25°C	30	3	5
	60	0	3
	90	0	0

The effect of stratification on the germination of both species was investigated by imbibing seed on moist filter paper for 24 hours and then incubating them at 5° and 25°C for 0, 30, 60 and 90 days respectively. After incubation the seed was germinated under standard conditions.

The results presented in Table 4 show that incubation of seed at 25°C decreased germination significantly. Stratification of seed of both species at 5°C for 30 days increased germination. However, longer periods of stratification did not increase germination further. The effect of stratification is apparently to increase the ability of cotyledons to split the coat in *L. daphnoides* and the radicle to pierce the coat in *P. compacta.*

Light treatments

Experiments with red and far-red light treatments supported the contention (Horn, 1962) that light does not influence the germination of proteaceous seed.

Oxygen treatments

The effect of the seed coat on free exchange of oxygen was investigated by germinating seeds of *P. compacta* and *L. daphnoides* in air, oxygen and nitrogen. The seed was placed on moist sand in 500 ml flasks. The flasks were evacuated and then flushed with the appropriate gas. At 4-day intervals the gas was renewed and germinated seed removed. Care was taken to ensure that atmospheric pressure was not exceeded in the flasks.

TABLE 5

THE EFFECT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* OF INCUBATING SEED IN AIR, PURE OXYGEN AND PURE NITROGEN.

Figures are mean percentages of 4 replications of 20 seeds.

TREATMENT	*PROTEA COMPACTA*	*LEUCADENDRON DAPHNOIDES*
AIR	47 ± 17	12 ± 7
PURE OXYGEN	72 ± 7	85 ± 14
PURE NITROGEN	0	0

Oxygen increased germination (Table 5), the effect being more marked in *L. daphnoides* than *P. compacta.* No germination was recorded in the absence of oxygen and when after 44 days the nitrogen was replaced by oxygen *L. daphnoides* gave a 55% germination response, indicating that seed had not suffered adversely in the absence of oxygen. *P. compacta* seed, however, failed to germinate. These results clearly suggest that in both species the seed coat may act as a barrier to gaseous diffusion and hence impose dormancy. Furthermore it seems most likely that the deleterious effect of prolonged soaking (Tables 2 and 3) is due to the resistance of the water layers to the diffusion of oxygen. The difference in response to oxygen, after nitrogen treatment, may be related to fundamental differences in the metabolism of *P. compacta* and *L. daphnoides* seed.

Applied hormones

Growth promoters such as kinetin and gibberellic acid can substitute for the chilling requirement of certain seeds (Webb and Dumbroff, 1969; Baskin and Baskin, 1970). In order to determine whether they can bring about a similar effect in the seed of *P. compacta* and *L. daphnoides*, seed was soaked for 24 hours in each of a range of solutions of benzyladenine (BA) and kinetin (1, 10, 50 mg/l), and gibberellic acid (1, 10, 100 mg/l).

Table 6

THE EFFECT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* OF SOAKING SEED IN KINETIN, BENZYLADENINE AND GIBBERELLIC ACID.

Figures are mean percentages of 4 replications of 10 seeds after 72 days.

CHEMICAL	CONCENTRATION	*PROTEA COMPACTA*	*LEUCADENDRON DAPHNOIDES*
	Control	57 ± 3	20 ± 2
Kinetin	1 mg/l	67 ± 5	13 ± 1
	10 mg/l	78 ± 1	33 ± 4
	50 mg/l	58 ± 3	30 ± 2
Benzyladenine	1 mg/l	72 ± 3	35 ± 3
	10 mg/l	54 ± 5	20 ± 2
	50 mg/l	76 ± 2	10 ± 1
Gibberellic Acid	1 mg/l	62 ± 3	23 ± 2
	10 mg/l	68 ± 1	30 ± 2
	100 mg/l	66 ± 1	23 ± 3

Although germination in both species can be increased by treatment with the three growth promoters, the species differ in their responses (Table 6). Kinetin (10 mg/l), BA (50 mg/l) and GA_3 (10 mg/l) elicit highest germination in *P. compacta*, whereas in *L. daphnoides* kinetin (10 mg/l), BA (1 mg/l) and GA_3 (10 mg/l) are equally effective. These results agree with those obtained with excised embryos under sterile conditions (Van Staden *et al.*, 1972).

The effect of applied hormones may be to increase radicle extension in *P. compacta*, as has been shown to occur in lettuce by Haber and Luippold (1960) and in *Acer pseudoplatanus* by Pinfield and Stobart (1972). In *L. daphnoides* the effect may be to promote cotyledon expansion as found by Ikuma and Thimann (1963) in lettuce; Kursanov, Kulaeva and Mikulovich (1969) in pumpkin and Esashi and Leopold (1969) in *Xanthium*.

Conclusions

The germination responses of seed to a wide range of treatments show that both the coats and embryos could contribute to the dormant condition in *P. compacta* and *L. daphnoides*.

Although inhibitors are leached from intact seed, no evidence could be found that they are actually involved in the regulation of germination, or that their leaching is a prerequisite for germination. In addition the covering structures do not appear to restrict the leaching of such compounds from the embryo.

In *P. compacta* the seed coat appears to mechanically restrict radicle elongation, and to a lesser extent, to retard oxygen uptake. These effects are overcome to a greater or lesser degree by scarification, high oxygen tensions and stratification. The effect of stratification may be due to physical changes in the covering structures, enabling the radicle to emerge more readily, or to chemical changes in the embryo enabling the radicle to develop sufficient thrust to pierce the coat.

In *L. daphnoides* the seed coat imposes dormancy by acting as a barrier to oxygen diffusion to the embryo. Scarification treatments which broke that barrier, as well as high oxygen tensions applied to intact seed resulted in dramatic increases in germination. The poor germination obtained after prolonged soaking and leaching may be due to an increased barrier to oxygen brought about by the over-abundance of water. Stratification increases germination, an effect which can perhaps be attributed to the indirect influence of low temperature on oxygen diffusion to the embryo. Wareing (1969) has stressed that for stratification to be successful seeds must be fully imbibed and have adequate aeration. It is postulated that chilling treatments lead to physical changes in the covering structures which then allow greater penetration of oxygen. This in turn leads to increased metabolic activity, resulting in changes in hormone levels that can promote radicle elongation in *P. compacta* and cotyledon expansion in *L. daphnoides*. Both these growth phenomena have previously been shown to be affected by hormones (Ikuma and Thimann, 1963; Pinfield and Stobart, 1972), while in the present study gibberellins and cytokinins have been shown to increase germination. It is possible that the effect of oxygen in increasing germination is mediated by changes in endogenous hormone levels. This possibility is at present under study.

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